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FRAGRANCE IN RELATION TO POLLINATION OF *ONCIDIUM SPHACELATUM* AND *TRICHOCENTRUM OERSTEDII* (ORCHIDACEAE) IN THE SOCONUSCO REGION OF CHIAPAS, MEXICO

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ABSTRACT. Flowers of *Oncidium sphacelatum* and *Trichocentrum oerstedii* were observed during several days at two sites in the Soconusco region of Chiapas, Mexico, to obtain details of seed set and insect visitation and to capture and identify potential pollinators. Fragrance samples from flowers of both orchids were taken for chemical analysis. No insect activity was observed for *T. oerstedii,* and no seed capsules had been produced. The bee, *Centris* (*Hemisiella*) *trigonoides,* although the most consistent visitor to the flowers of *O. sphacelatum,* did not participate in pollination. Single *Centris* (*Paracentris*) *mexicana* bees visited a few flowers once a day, and the authors trapped one bee with an *O. sphacelatum* pollinia present on the dorsal surface of the thorax. This orchid species presented a single seed capsule at the end of the flowering period. Different pollination strategies proposed for the two genera in Oncidiinae are discussed. Analysis of hexane extracts of flowers revealed that the dominant component of both species was a mixture of unsaturated and saturated hydrocarbons (C25–C31) as wax constituents. Although the fragrance of *O. sphacelatum* was characterized by zingerone, and the distinguishing component of the fragrance of *T. oerstedii* was syringaldehyde, both species produced relatively little scent. The timing of peak scent production was variable and did not necessarily coincide with insect visitation, suggesting that fragrance is not an important factor in the process of pollination.

Key words: pollination strategy, *Oncidium, Trichocentrum, Centris trigonoides, Centris mexicana,* syringaldehyde, zingerone

INTRODUCTION

The genus *Oncidium,* previously notorious for its extremely variable vegetative morphology and adaptation to differing altitudes and habitats (Stewart & Griffiths 1995, Pridgeon 2000) recently has been divided among various genera (Pupulin 1995, Williams et al. 2001). Controversy still exists, however, as to the final taxonomic position of many species.

Oncidium sphacelatum Lindley is a Central American orchid unflatteringly referred to locally as "sausage and egg" for its vivid yellow flowers with brown or dark wine-colored marks. The flowers are produced from the last week of December through the end of March, depending upon altitude and habitat. This attractive medium-sized orchid, with flattened, ribbed pseudobulbs and elongated, soft, pale green leaves, is still fairly common below 1000 m. Found in coffee plantations and remaining fragments of tropical evergreen and semi-deciduous forests in the Soconusco region in southeastern Mexico, *O. sphacelatum* is often grown as an ornamental plant in rural gardens.

Trichocentrum oerstedii was previously and erroneously named *Lophiaris carthagenensis* (Jacq.) Braem and *Oncidium carthagenense* (Jacq.) Sw. It presents a very different morphology, with a vestigial pseudobulb and single, succulent, dark green leaves resembling donkey ears, which is the name given to this orchid by local people. *Trichocentrum oerstedii,* more widely distributed than *O. sphacelatum,* is found from Florida to Brazil. In the Soconusco region, *T. oerstedii* has become particularly adapted to coffee plantations, where it presents an incongruous sight, with the large, clumsy-looking native orchid growing on the slender trunks and branches of coffee trees, which are an introduced species.

The subtribe Oncidiinae encompasses a great diversity of pollination strategies, but few reports feature the pollination of *Oncidium.* Parra-Tabla et al. (2000) describe *O. ascendens* Lindl., now *Trichocentrum ascendens* (Lindl.) M.W.Chase & N.H.Williams (Williams et al. 2001), as having a low pollination rate even under favorable conditions. This orchid produces flowers without nectar, which are primarily pollinated by *Trigona nigra,* a social bee that harvests resins for nest construction. A secondary pollinator is a *Centris* species. Yet to be confirmed is whether this orchid produces oils or resins, or merely imitates the flowers of other species that do.

The literature proposes three deceptive pollination mechanisms for the genus *Oncidium,* de-

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scribed in detail by Van der Cingel (2001). The first is pollination by anthophorid bees of the genus *Centris,* which are presumed to collect oils and/or pollen and to use the flowers as a focal point for meeting females. The male bees defend their territory against other flying insects, and Ackerman (1986) has suggested that *Oncidium* flowers resemble insects and thereby incite territorial aggression when they flutter in the breeze. The pollination mechanism depends upon the head-on attack by the male *Centris* bees, whereupon the pollinium adheres to the frons of the insect and is then carried to another flower (Van der Pijl & Dodson 1966). The second mechanism depends on the resemblance of the fleshy, warty calli on the lip to food bodies (Stewart & Griffiths 1995, Pridgeon 2000), otherwise referred to as false pollen, to which female *Centris* bees are visually attracted. Finally some *Trichocentrum* and *Oncidium* species, many of which have now been relocated into the genus *Tolumnia,* imitate the flowers of malpighiaceous vines that produce oils in paired sepaline glands and probably attract the bees by ultraviolet reflection from the petals. The orchid imitators, however, offer nothing to their visitors (Van der Cingel 2001, Silvera 2002). The production of oils by neotropical Oncidiinae is discussed amply by Silvera (2002).

In discussing the fragrance production by flowers of the genus *Oncidium,* Kaiser (1993) mentioned that species with yellow flowers with brown dots or splashes tend to emit aromas containing 2-amino benzaldehyde and 3-phenylpropyl alcohol. Another group with similar flowers produces aromas with tones of aniseed and honey, and the large yellow-flowered oncidiums produce fragrances in which β-ionone predominates. Yet the fragrances of a relatively small proportion of the species of this genus have been analyzed. The two species in this study do not produce strong fragrances, and the fragrance of *Oncidium sphacelatum* is barely perceptible to the human nose, and *Trichocentrum oerstedii* produces a light, resinous aroma.

The pollination of most orchid species is a specialized process, dependant upon one or a very few species of insects (or in some unusual cases, birds). Such a pollination strategy is prone to failure because of resource limitation and/or pollinator limitation and small changes in environmental conditions. Even if pollination is achieved, environmental factors may then interfere with the chances of successful seed germination and the persistence of young plants (Koopowitz 2001).

This study sought to analyze the components, quantities, and timing of fragrance production for *Oncidium sphacelatum* and *Trichocentrum oerstedii* and relate them to observed pollination activity at two sites in the Soconusco region in Chiapas Mexico.

Materials and Methods

Study Sites

The two sites selected for the study in the Soconusco region in the state of Chiapas, Mexico, are typical of the general environmental conditions of the region, in which no undisturbed forest remains. The study was carried out between mid-January and the beginning of February in 2003, during the dry season and peak flowering period for these two species of orchids.

Site 1. "El Soconusco"

The Regional Botanical Garden "El Soconusco," at 80 m in the municipality of Tuzantán in Chiapas, contains a well established collection of low-altitude, local species of orchids. Average temperatures and relative humidity during the experimental period occurred at 11.30 hours, 34°C, and 60% and at 17.30 hours, 30°C, and 65%, respectively. This site, located in the municipality with the greatest native tree cover in Soconusco, is surrounded by extensive traditional cocoa plantations with a diversity of native trees as shade.

Site 2. "Santo Domingo"

The orchidarium "Santo Domingo," at 900 m in the municipality of Unión Juárez, contains a collection of middle-altitude orchid species from the region. Average temperatures and relative humidity occurred at 11.30 hours, 36°C, and 35% and at 17.30 hours, 22.5°C, and 85%, respectively. The site is located at the edge of coffee plantations with species of *Inga* as shade trees and with occasional native forest trees.

Both coffee and cocoa plantations, with their shade trees, effectively replace what was the original tropical, humid forest and act as refuges for the remaining biodiversity of the region.

Collection of Volatiles

Samples of the fragrances of mature flowers of *Oncidium sphacelatum* and *Trichocentrum oerstedii* were obtained during three days at each of the two sites, Domingo and Tuzantán. Attempts were made to collect samples of volatiles using the "headspace technique," but this technique proved to be insensitive to the small quantities of fragrance produced. Samples then were collected in-situ at 11.00 hours and 17.30 hours, and 30 grams of flowers were placed into vials containing 100 ml of hexane. The samples

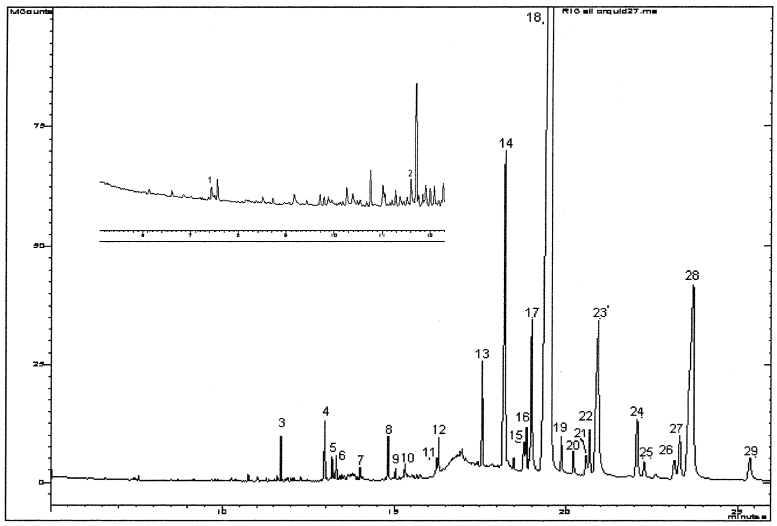

FIGURE 1. Gas chromatogram of the volatile components of *Trichocentrum oerstedii.*

were taken to the laboratory, and extraction was completed after samples were soaked for 12 hours at 25°C. The hexane then was passed through a strainer and stored at 5°C until use. A few of the hexane extracts also revealed quantities too small to be analyzed.

Chemical Analysis

Analysis of the extracts was performed using a Varian Star model 3400 CX GC. ADB-5 column (30 m × 0.25 mm ID). The temperature was programmed for 50°C (held for 2 minutes) to 250°C at 15°C/minute. The injection port temperature was held at 200°C. The sample was heated in the injector to 200°C for 5 minutes before crushing the glass capillary. The GC was coupled to a Varian Saturn 4D mass spectrometer and integrated data system. Ionization was by electron impact at 70 eV (electron-volt), 230°C. The amount of each compound was calculated from the peak area (FIGURES 1, 2). The relative percentage of the components was calculated from the sum of the recorded peaks. Mass spectral identifications were confirmed wherever possible by comparison of retention

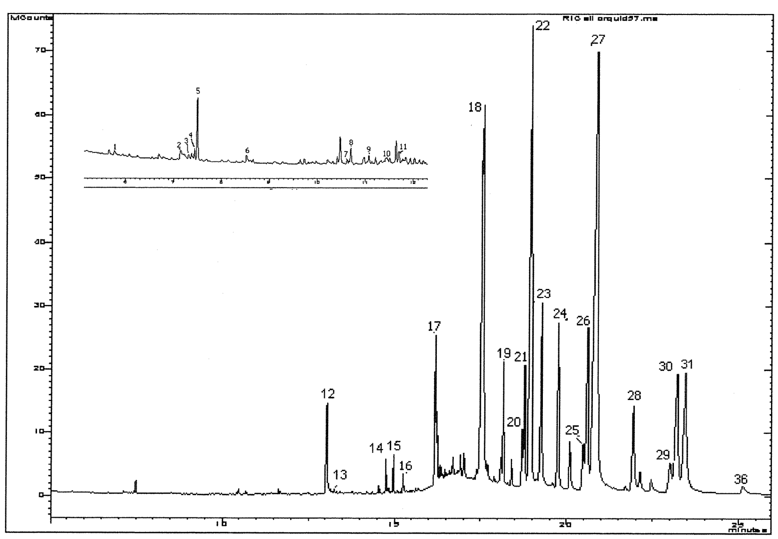

FIGURE 2. Gas chromatogram of the volatile components of *Oncidium sphacelatum.*

times and mass spectra with those of synthetic standards. Where pure standards were not available, identification was based on comparison with spectra from the National Institute of Standards and Technology (NIST) 2001 computer library.

Pollination and Visiting Insects

Observations were made simultaneously with the attempts at volatile sampling (headspace technique), but using different inflorescences. Flower samples also were collected from inflorescences that were not under direct observation. Full-day observations also were carried out on non-sampling days. Attempts were made to film visiting insects using a digital video camera (Sony Handycam DCR-TRV17) seated on a tripod; and where possible, samples of candidate pollinating insects were trapped for identification. In Site 2 with a greater number of inflorescences, counts were made to establish an average number of flowers per inflorescence. After several days of observations, a detailed destructive analysis was made of the inflorescence where most insect activity was observed and of the oldest inflorescence with a seed capsule starting to swell. The following conditions were noted: flower complete; pollinarium cap moved with pollinarium present; pollinarium cap moved and pollinarium absent; pollinia present on stigmatic surface; flower damaged, flower immature. Complete mature flowers were observed under ultraviolet light to test for the appearance of nectar guides, insect forms, etc., that might help explain the behavior of insect visitors.

RESULTS

Chemical Analysis

The chemical contents of *Oncidium sphacelatum* and *Trichocentrum oerstedii* are provided in TABLE 1. Analysis revealed that the major chemical component of the *O. sphacelatum* scent was a mixture of wax-type saturated hydrocarbons (C25–C31) followed by a small amount of a mixture of aldehydes, alcohols, and terpenes. Zingerone (1.5%) was identified as the main volatile component. The main components of the *T. oerstedii* scent also were wax-type saturated hydrocarbons (C25–C31), comprising 95% of the total relative amount of constituents. Analysis identified as fragrance constituents a very small amount of a mixture of aldehydes, alcohols, and terpenes, with syringaldehyde as the major component (2.3%). The headspace technique was not suitable for the collection of the volatile components, because the amount of these compounds was too small.

A quantitative analysis was made to see if the amount of volatiles released in the morning (11.00 hours) differed from those in the afternoon samples (17.30 hours). Specifically, the amounts of zingerone and syringaldehyde released by *Oncidium sphacelatum* and *Trichocentrum oerstedii,* respectively, were analyzed (TABLE 2). The amounts were so variable that no pattern was discernable; and in the case of *O. sphacelatum,* no relation could be found between the amount of zingerone present and the presence of *Centris mexicana,* the bee seen to visit in the morning, toward midday.

Pollination and Visiting Insects

Eight inflorescences of *Oncidium sphacelatum* and three of *Trichocentrum oerstedii* were observed in Site 1. Present in Site 2 were fourteen fully developed inflorescences of *O. sphacelatum* and four of *T. oerstedii.* Flower numbers per sampled inflorescence were 95, 99, 54, and 98 for *O. sphacelatum* and 12, 17, 48, 36, and 53 for *T. oerstedii.*

Insect visitors to *Trichocentrum oerstedii* were very few. No candidate pollinators were seen, and no seed capsules were produced. Insect visitors to *Oncidium sphacelatum* were very few in Site 1; and most of the data presented in this paper originates from Site 2.

In Site 2 (Santo Domingo, 900 m), daylight began at 06.00 hours, and the sun rose at 07.00 hours. The first rays of sunlight reached flowers of *Oncidium sphacelatum* at ca. 08.47 hours, and flowers thus illuminated were seen to be most attractive to insect visitors. The earliest visits were made by small meliponid bees at 08.30 hours; these bees were seen to be casual visitors and most interested in extrafloral nectar produced by flower buds, especially those of a nearby *Encyclia cordigera* (Kunth) Dressler (Orchidaceae). Small native trigonid bees started to visit at 08.45 hours; these rasped the surface of the petals but were not seen to come into contact with the column. Another casual visitor was the minute, light brown, semi-transparent bee, *Trigona* (*Tetragonisca*) *angustula* Lepeletier, locally known as doncella. Activity, which declined rapidly during cloudy periods, was greatest between 09.00 and 13.30 hours on sunny days.

Three of the observed insect visitors were designated as potential pollinators of *Oncidium sphacelatum.* The first was present on several days and remained in the vicinity of the flowers during the morning. These bees constantly hovered in front of selected flowers, particularly those exposed to full sunlight, and very occa-

TABLE 1. Fragrance components of *Oncidium sphacelatum* and *Trichocentrum oerstedii.*

Species	Peak	Compound	%
Oncidium sphacelatum	1	2-Pentyl furane**	<1.0
	2	Nonanal*	<1.0
	3	β-Ionone*	<1.0
	4	Zingerone*	1.5
	5	Unknown	<1.0
	6	Sesquiterpene	<1.0
	7	Unknown	<1.0
	8	Methyl palmitate**	<1.0
	9	Methyl linoleate**	<1.0
	10	Unknown	<1.0
	11	Pentacosadiene**	<1.0
	12	Pentacosene**	<1.0
	13	Pentacosane*	4.5
	14	Sesquiterpenoide	52.0
	15	Hexacosane*	<1.0
	16	Branched hydrocarbon	<1.0
	17	Heptacosadiene**	<1.0
	18	Heptacosene**	1.4
	19	Heptacosane*	9.1
	20	Octacosane*	2.2
	21	Squalene	<1.0
	22	Nonacosadiene**	<1.0
	23	Nonacosene**	1.9
	24	Nonacosane*	16.5
	25	Triacontane*	1.3
Trichocentrum oerstedii	1	Benzaldehyde*	<1.0
	2	*p*-Cresol*	<1.0
	3	Guiacol**	<1.0
	4	Linalool*	<1.0
	5	Nonanal*	<1.0
	6	β-Gurjunene**	<1.0
	7	Unknown	<1.0
	8	A-Guaienene**	<1.0
	9	A-Patchoulene**	<1.0
	10	γ-Gurjunene**	<1.0
	11	Syringaldehyde*	2.3
	12	Patchouli alcohol**	<1.0
	13	Unknown	<1.0
	14	Methyl palmitate**	<1.0
	15	Methyl linoleate**	3.3
	16	Unknown	7.9
	17	Branched hydrocarbon	2.7
	18	Pentacosadiene**	1.5
	19	Pentacosene**	2.9
	20	Pentacosane*	16.6
	21	Unknown	5.7
	22	Hydrocarbon	4.3
	23	Heptacosadiene**	1.4
	24	Heptacosene**	5.6
	25	Heptacosane*	26.8
	26	Hydrocarbon	3.1
	27	Nonacosadiene**	1.4
	28	Nonacosene**	6.1
	29	Nonacosane*	6.8

Note: Chemical identification: * = synthetic standards, ** = computer library.

TABLE 2. Amounts of zingerone produced by *Oncidium sphacelatum* and syringaldehyde produced by *Trichocentrum oerstedii.*

Species and fragrance	Samples	Morning (11.00 hours) ng	Afternoon (17.30 hours) ng
Oncidium sphacelatum			
Zingerone	1	77.98	839.56
	2	525.96	20.85
	3	—	29.40
	4	—	103.05
Trichocentrum oerstedii			
Syringaldehyde	1	0.44	44.98
	2	48.09	9.98
	3	239.35	20.80
	4	—	1.97
	5	—	222.25
	6	—	80.87

Note: ng = nanograms.

TABLE 3. Destructive analysis of selected inflorescences of *Oncidium sphacelatum* at Site 2. A = most activity carried out by candidate pollinators. B = oldest inflorescence, with one seed capsule in early stages of development.

Inflorescence	A	B
Total no. flowers	57	43
Flower mature, untouched	14	9
Anther cap missing or displaced, pollinarium present	5	6
Anther cap present but displaced, pollinarium absent	2	0
Anther cap and pollinarium absent	21	8
Pollinarium present on stigmatic surface	0	3
Flower damaged or withered	1	20
Flower immature	14	0

sionally lunged at the flowers and followed with sweeping circles before returning to hovering. Sometimes they perched on the upper surface of the leaves of the orchid. Occasional conflicts were observed between individual bees engaged in the same activity, which usually ended with one of the bees leaving the site; there were never more than three bees of this species present at any one time. One individual was trapped (19 January 2003); it did not carry a pollinium and was later identified as *Centris* (*Hemisiella*) *trigonoides* Lepeletier. This species was observed only in the orchidarium at Santo Domingo (Site 2). This medium-sized bee has a beige-gray thorax and a black abdomen. A small yellow patch on the upper part of the frons, at first sight, can easily be confused with an attached pollinium. Two of the three capsules produced in Site 2 were formed in the area most frequented by these bees. Flowers of *O. sphacelatum* are seen as completely black under UV light, which was absorbed by the surface of the petals and sepals. Little or no indication was given of UV reflecting guides or insect forms appearing under UV radiation, as suggested by Van der Cingel (2001). Entirely black bodies moving in the breeze, however, could have led *C. trigonoides* to interpret them as conspecifics or other insects. The energy economy of this bee presents an interesting scenario; it did not seem to forage or consume anything during the very active visits lasting several hours.

The second candidate pollinator of *Oncidium sphacelatum* was a very rapid flying, medium-sized, black bee, identified as *Centris* (*Paracentris*) *mexicana* Smith, which made occasional brief and very precise visits mostly between 10.30 and 11.30 hours; one visit was registered at 13.15 hours. These bees arrived singly, only one per day (possibly always the same individual), and flew directly to the center of a very few selected flowers in rapid succession, and grasped the central area of the flower. The bees were present at the site for no more than 2 minutes. The nature and timing of these visits suggest traplining, but it is uncertain whether *O. sphacelatum* is the main attractant or imitates another attractive species in the vicinity. The few seconds of video coverage obtained was insufficient to determine exactly what the bee was doing at each flower. One individual was captured (19 January 2003) in the orchidarium at Santo Domingo, with a pollinarium from *O. sphacelatum* on the upper part of the frons. One of the three capsules produced in Site 2 was formed in the area most frequented by these bees. This species was not observed in the botanical garden in Tuzantán (Site 1), although in subsequent years, capsule formation has been observed there.

The third species of bee was observed on only three occasions (twice in Site 2 and once in Site 1) toward the end of the flowering and experimental period. Visits were made at ca. 20-minute intervals between 09.30 and 12.30 hours. This was another medium-sized species with a very hairy, golden brown thorax. Individuals hovered in front of selected flowers and attacked them vigorously. The visits were so few and short that it was not possible to capture or identify these bees, to mark visited flowers to check for subsequent pollination, or to see whether these bees carried pollinaria.

The results of the destructive analysis of two selected inflorescences of *Oncidium sphacelatum* are presented in TABLE 3. These data indicate that male success, at 40.35% (23 flowers

with pollinaria removed of a total of 57), is notable for the first inflorescence, where pollinators were most active, and low for the second and oldest inflorescence at 18.6% (8 flowers with pollinaria removed of a total of 43). Pollinaria obviously were moved, transported, or lost; and some probably fell to the ground; only once was a pollinarium seen attached to a bee. The first inflorescence still carried unopened flowers and presented zero female success. The second inflorescence, which was in its final stages (despite lower male success), presented one seed capsule and a total of 7% female success. The net result of a few visits in Site 1 and consistent visits by three candidate pollinators in Site 2 was a very low rate of seed set, 0% in Site 1 and 0.25% in Site 2 (average of 86.5 flowers per inflorescence and 14 inflorescences) giving a total of ca. 1211 flowers with 3 seed capsules forming. As mentioned above, the potentially very large number of seeds in each capsule can be seen as compensating for the very low rates of pollination typical of the entomophilic orchids.

Discussion

The literature mentions various pollination mechanisms for the genus *Oncidium,* and the results of this study show that territorial aggression (males) and possibly oil collection and food deceit (females) are employed by *O. sphacelatum* in Soconusco. In the case of *Centris mexicana,* the bee flies directly to the center of the flower to collect oils directly, or the insect initially is deceived by the calli on the lip, which may resemble stamina, otherwise referred to as false pollen, to which female *Centris* bees are attracted. By means of this behavior, one of the bees in this study exited a flower with a pollinium attached to the dorsal surface of the thorax.

Centris trigonoides males engage in aggression with the flowers presumably incited by their resemblance to a conspecific male. In this case, the pollination mechanism depends upon the head-on attack by the male bee, whereupon the pollinaria adhere to the frons of the insect and then are carried to another flower. In these experiments, however, the bees rarely contacted the flowers, and none of the bees were seen to be carrying pollinaria. Another suggested mechanism, the imitation of malpighiaceous vines, possibly was occurring here, but the bees were not seen to visit nearby flowering "nance" trees, *Byrsonima crassifolia* (L.) Kunth, which belong to that family and have flowers of a similar color to those of the orchid.

As mentioned by Van der Cingel (2001), *Centris* bees fly very fast and are therefore difficult to observe. The same *Centris* bee may have visited every day, possibly traplining between patches of *Oncidium sphacelatum* and perhaps other species. Only once was a bee seen carrying a pollinarium; therefore most of this activity is superfluous to the orchid. Although the possibility of meeting females could be compensatory, *C. trigonoides* did not appear to benefit from the extended attention paid to the flowers, raising the question of energy budget for these bees. How did they fuel these extended and energetic periods of activity?

The chemical analysis of the fragrance of *Oncidium sphacelatum* and *Trichocentrum oerstedii* showed that both species contain similar mixtures of unsaturated and saturated hydrocarbons (C25–C31). *Oncidium sphacelatum* appeared to be characterized by zingerone, a pungent essence of ginger, which has been found in the wild orchid *Bulbophyllum patens* King as an attractant of male fruit flies of several *Bactrocera* species (Diptera: Tephritidae) (Ritsuo & Keng Hong 2000). *Trichocentrum oerstedii* seems to be characterized by syringaldehyde, a phenolic compound derived from lignin decomposition and also a volatile component of several plants, for example the Chinese herb *Codonopsis pilosula.* It has been found as an attractant for *Scolytus multistriatus* (Coleoptera: Scolytidae) (Meyer & Morris 1967). This compound has not been previously found in orchids.

No relationship could be established between the diurnal changes in the production of key components of the fragrances produced and pollinator visits. Fragrance samples from both orchid species were too varied, and pollinator visits were too few in the case of *Oncidium sphacelatum* or absent in the case of *Trichocentrum oerstedii.* Variation in floral fragrance compounds might be a pollination strategy that disrupts associative learning processes and inhibits pollinator ability to recognize non-rewarding flowers (Moya & Ackerman 1993). Other mechanisms might be involved in the pollination of these two species, such as flower color, as reported in the pollination success of *Weigela middendorffiana* by bumble bees (Ida & Kudo 2003). Most probably the initial stimulus is the color of the flower; and at close range, the weak fragrances produced by the orchids serve to guide visiting insects toward the source of oils.

The scarcity of bees renders difficult the logical sequel to this study, which would be to capture several bees; to then test with electroantennograms for the active components in the fragrances; then to dissect the flower and find out which area "smells" and observe the behavior of the bees in relation to the "smelly" area. The acquisition of video footage also is difficult.

Survival strategies for orchids may include

emphasis on asexual, i.e., vegetative reproduction that enables the cloning of successful genotypes to extend existing populations within available sites, as discussed in the case of bromeliads (Benzing 2000). Many orchids have responded to environmental changes and instability, leading to the reduction in pollination events, by becoming autogamous, which in the long term can reduce genetic diversity and the flexibility of response available to populations. The production of showy flowers and expensive rewards to attract insect visitors to facilitate sexual reproduction may then become a mere secondary option, involving great investment on behalf of the orchid and few chances of success under present-day conditions of environmental deterioration and biodiversity reduction. Ackerman (1989) and Nilsson (1992) have discussed various reasons for the characteristic low rates of visitation and seed set in orchids, wherein visitation rates for orchids offering rewards may be close to visitation rates for deceptive or simply rewardless orchid flowers. Another factor is the compensatory large number of seeds produced in the average orchid seed capsule, making rare and unpredictable pollination events very rewarding for the orchid. Within this confusing scenario, the process of selection and coevolution between pollinator and plant may deteriorate or become obsolete. Then chaotic, unspecialized visitation by various insect species, or zero visits, may become the norm. Observations in the Soconusco region have shown that percentage pollination, considering individual flowers, is 0.7% for *Oncidium sphacelatum* and 0.05% for *Trichocentrum oerstedii* (Damon unpubl. data). The orchid family is undergoing a process of speciation, and much variability exists within presently established species. Local races may be very different; and variation in fragrance content, to mention but one aspect, is notable even between individuals within the same population (Damon et al. 2002). Although this strategy may help orchids keep their options open, the general trend may be toward deterioration and confusion in the pollination process. Confirmation awaits long-term data.

In the light of these results, we pose the following questions for further study. Are pollinators attracted to *Oncidium sphacelatum* by food deception or territorial aggression, or, as suggested by our results, a mixture of both? Which part of the flower of these two orchid species (*O. sphacelatum* and *Trichocentrum oerstedii*) smells? Is it the oils themselves, or are these weak fragrances produced by osmophores in the body of the flower? Finally, is the "cost" of producing the oils or resins worth it, given the very low rate of pollinator visitation, pollination, and capsule production?

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